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Life history of the ground beetle *Diacheila polita* (Faldermann, 1835) (Coleoptera: Carabidae) in Subarctic and Arctic of North Europe and West Siberia

Жизненный цикл жужелицы *Diacheila polita* (Faldermann, 1835) (Coleoptera: Carabidae) в субарктике и арктике Северной Европы и Западной Сибири

B.Yu. Filippov, N.A. Zubrii
Б.Ю. Филиппов, Н.А. Зубрий

N. Laverov Federal Center for Integrated Arctic Research of the Ural Branch of the Russian Academy of Sciences, Northern Dvina Emb. 23, 163000 Arkhangelsk, Russia. E-mail: fby@yandex.ru

Федеральный исследовательский центр комплексного изучения Арктики им. Н.П. Лаверова УрО РАН, наб. Северной Двины. 23, 163002 Архангельск, Россия.

KEY WORDS: Life cycle, ground beetle, photoperiod, temperature conditions, Arctic, adaptation.

КЛЮЧЕВЫЕ СЛОВА: Жизненный цикл, жужелицы, фотопериод, температура, Арктика, адаптация.

ABSTRACT. The patterns of sex and age structure, seasonal activity of *Diacheila polita* under photoperiod and temperature conditions were studied in the North Europe and West Siberia within three bioclimatic zones: forest-tundra, southern tundra and typical tundra. A total of 7,963 adults and 24 larvae were collected using pitfall traps. All adults were dissected to determine their reproductive states. Adults of *D. polita* were active from the end of June until the beginning of September generally with one peak in August. Newly emerged and immature beetles had been catching in traps, from June or in the beginning of July. Mature adults had been registering from the end of June. At the end of August, more than 70% of the studied populations were represented by mature adults. Larvae of *D. polita* had been catching from the second half of July to the beginning of August in tundra. The life cycle of *D. polita* is described as obligate-biennial late summer iteroparous. Seasonal mature adults activity is depended on daylight hours duration but not correlated with temperature conditions. Activity of mature females was more synchronized with photoperiod conditions than of mature males. The reduction of daylight hour's duration stimulated adult beetles to maturation and reproduction, and reaching the peak activity of individuals at the time when the daylight duration reaches 17–15 hour in typical tundra and 16–15 hour in forest-tundra and southern tundra.

РЕЗЮМЕ. Изучены закономерности половозрастной структуры и сезонной активности под действием фотопериода и температуры *Diacheila polita* в Северной Европе и Западной Сибири, в пределах трёх биоклиматических зон: лесотундре, южной тундре и типичной тундре. Всего с помощью ловушек было собрано 7963 имаго и 24 личинки. Все имаго были вскрыты для определения их репродуктивного состояния. Актиность *D. polita* длится с конца июня до начала сентября, как правило, с одним пиком в августе. С июня – начала июля в ловушки попадали ювенильные, и иматурные жуки. Генеративные особи ловились с конца июня. В конце августа более 70% исследованных популяций были представлены генеративными особями. Личинки *D. polita* были собраны в тундре и попадались в ловушки со второй половины июля до начала августа. Жизненный цикл *D. polita* облигатно-двухгодичный позднелетний рецикличный. Сезонная активность генеративных особей зависит от длины светлого времени суток, но не зависит от температуры. Активность генеративных самок более синхронизирована с фотопериодом, чем у генеративных самцов. Сокращение продолжительности светлого времени суток стимулировало имаго к переходу в генеративное состояние и к размножению, пики активности особей приходились на время, когда продолжительность светового дня достигает 17–15 часов в типичной тундре и 16–15 часов в лесотундре и южной тундре.

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Introduction

Patterns of species distribution and range extension in most studies are explained by variability of environmental conditions or ecological niche of species [Bezdek, 2007; Jowetta, 2019, Knapp, 2019]. At the same time not all patterns of species expansions can be explain by variability of ecological factors [Schwartz, Ishchenko, 1971; Berman, 2007; Berman, Bulakhova, 2019], especially, in case of the absence of evident environmental limitations.

Field and laboratory experiments are supply data about environmental limitations in species distribution. One of the driven environmental factors affecting on adaptations of insects to Arctic and Subarctic are temperature conditions or shortage of heat supply [Balashov et al., 2011; Lopatina et al., 2012; Saska et al., 2014]. In this case lack of numerous species of insects in the Arctic is becoming clear. Among carabids beetles can transform their life cycle from one-year to two-year individual development for northward distribution [Filippov, 2007, 2008; Matalin, 2007, 2015]. At the same time, even carabid species with two-year life cycle have restrictions in distribution in high latitudes. Such pattern was detected for Holarctic species *Diacheila polita* (Faldermann, 1835), which is widely distributed in forest-tundra and tundra landscapes of Eurasia and North America [Lindroth, 1966, 1985]. Range of *D. polita* in Pleistocene reached North and West Europe up to British Islands. [Lindroth, 1985; Elias, 2010]. *D. polita* have a high density among carabids compositions in Subarctic but unclear causes are hold back its advance in high Arctic landscapes.

In this study, we explored (a) life-history characteristics of *D. polita* on the North Europe and West Siberia and (b) species seasonal activity under photoperiod and temperature conditions in the Arctic and Subarctic.

Table 1. Sampling localities and collected materials of *D. polita* in the North Europe and West Siberia
Таблица 1. Районы исследования и объём собранного материала по *D. polita* в Северной Европе и Западной Сибири.

Bioclimatic zonation	Locality, collecting period	GPS coordinates	Pitfall trap-days	Imago specimens (number)
Forest-tundra	Polar Ural, 10 km from Kharp settlement, 18.06-30.08.2017	66°90′ N 65°74′ E	24 852	169
Southern tundra (low shrub - Subzone E)	Kanin Peninsula, Shoyna settlement, 14.06-28.08.2005	67°49′ N 44°13′ E	28 350	119
Typical tundra (erect dwarf shrub - Subzone D)	Kolguev Island, Bugrino settlement, 01.07-08.09.2009	68°47′ N 49°17′ E	24 160	5 690
	Yugorskiy Peninsula, Amderma settlement, 17.06-07.09.2012	69°42′ N 61°41′ E	35 860	1 609
	Yamal Peninsula, Seyakha settlement, 28.06-02.09.2014	70°10′ N 72°30′ E	18 921	376
Total:			132 143	7 963

Materials and methods

Study sites and material collection

Field works were conducted by «local fauna» method by latitudinal gradient [Penev, 1996; Makarov, Matalin, 2009]. Specimens of *D. polita* were collected within 5 localities in North Europe and West Siberia (Table 1). Latitudinal gradient included locations within three bioclimatic zones: forest-tundra in Subarctic, southern tundra and typical tundra in Arctic (Table 1) [Walker et al., 2005].

Ground beetles were collected using pitfall traps [Barber, 1931; Heydemann, 1956] — 500 ml plastic cups with a trap hole diameter of 93 mm. In each site 10–25 traps were installed in lines with a distance of 10 m between traps and lines. For insects fixation 4% formaldehyde solution was used. The material was sampled from the traps once every ten days. As result, 1929 traps were installed for a total of 132,143 trap-days and 7,963 specimens of *D. polita* imago were sampled (Table 1). Larvae were recorded for the Kolguyev Is-

Table 2. Number of catching larvae of *D. polita* on Kolguyev Island in 2009.
Таблица 2. Количество личинок *D. polita*, собранных на острове Колгуев в 2009 г.

Instar larvae	I.07*	II.07	III.07	I.08	II.08	III.08	I.09	Total
II	0	1	2	0	0	0	0	3
III	0	4	12	1	0	0	0	20
Total	0	5	20	1	0	0	0	23

* I, II, III — ten-day periods.
* I, II, III — декады.

land (Table 2) and four third instar larvae were trapped in southern tundra of Kanin Peninsula: one larva in the middle of July and another three larvae in the last ten-day period of July.

The average air temperature and the polar day duration for studied localities for each ten-day period in June–September (when was *D. polita* was collected, see Table S1) were obtained from the records of the local meteorological stations (www.rp5.ru, my-calend.ru last accessed on 20th of August 2020).

Age determination and seasonal activity

The analysis of the age of both sexes in populations was performed by the method of Wallin [1989]. Adults of both sexes were dissected to determine the developmental stage of their gonads of the following five reproductive states: teneral, immature, mature, old-mature and spent (Table S2). Also, *D. polita* specimens with parasitic invasions by representatives of the class Gordiacea were excluded from the analysis because it was impossible to determine reproductive states of imago (Table S2).

Seasonal activity was described using the total number of caught specimens and peak of activity was registered in days when 50% of the total number of individuals were caught. Life-history patterns of *D. polita* were studied by seasonal variations of different reproductive states of specimens.

Statistical analysis

For data analysis the total number of specimens caught and their seasonal activity were used. Seasonal activity was calculated as the numbers of individuals trapped per 10 trap-days (ind/10 t-d) (Table S1).

One of questions of our research concerned the regulation of breeding period; therefore, the latitude of sampling localities was included as a covariate in the general linear model (GLM), which explored the sources of variation in seasonal activity of mature adults.

The relationships between seasonal activity of mature adults, mean temperature and daylight duration for each locality, were explored by calculating Spearman's rs correlation coefficient. Data analysis was conducted using both STATISTICA v.10 and PAST v.3.06 [Hammer, 2015].

Results

Seasonal activity and reproduction

Among study localities the entire activity period of *D. polita* was lasted from the end of June until the beginning of September generally with one peak in August (Table S2). Two peaks of adults activity were registered for Yugorskiy Peninsula in the end of July and in the end of August. Seasonal activity of different reproductive states of imago was visualized for Kolguyev Island (Fig. 1, for other studied populations see Table S2). Beginning of activity started after snow melt period in the end of June or in the beginning of July and newly emerged and immature beetles were predominated in study populations. Immature individuals were trapped until September in all studied populations. Activity peak of teneral beetles of *D. polita* was lasted from the end of August to the beginning of September. Mature

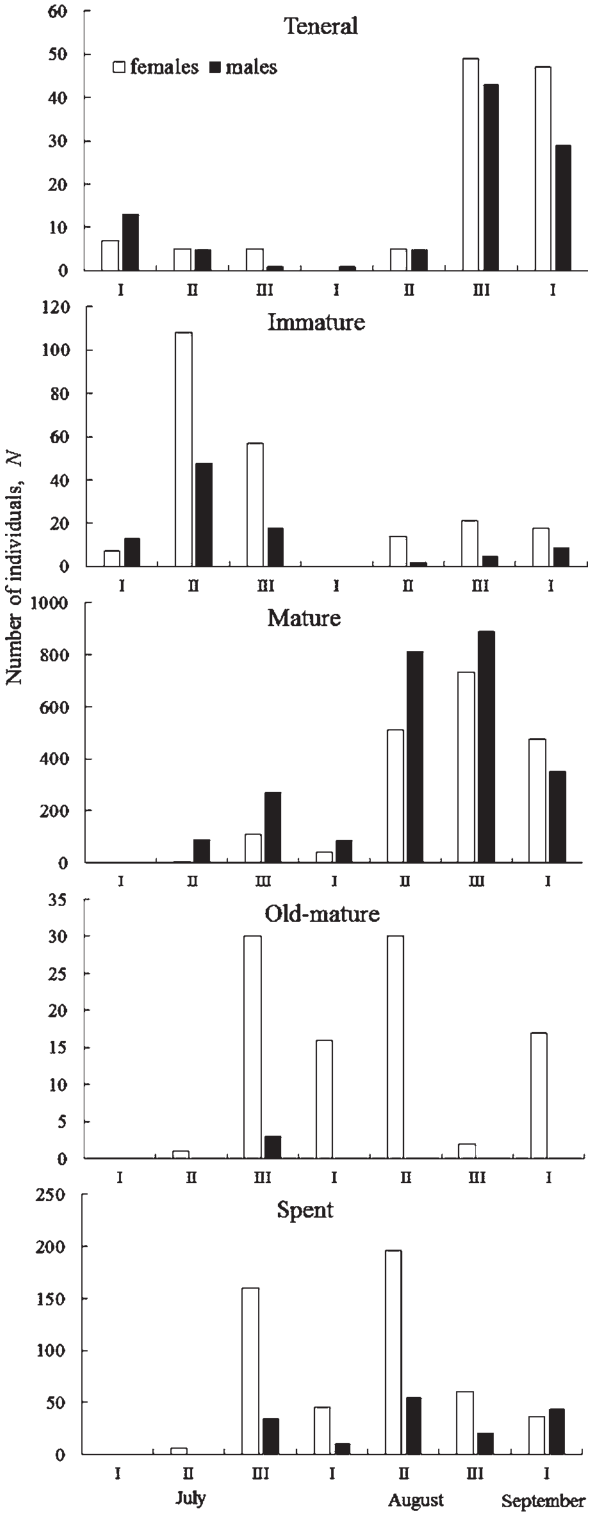
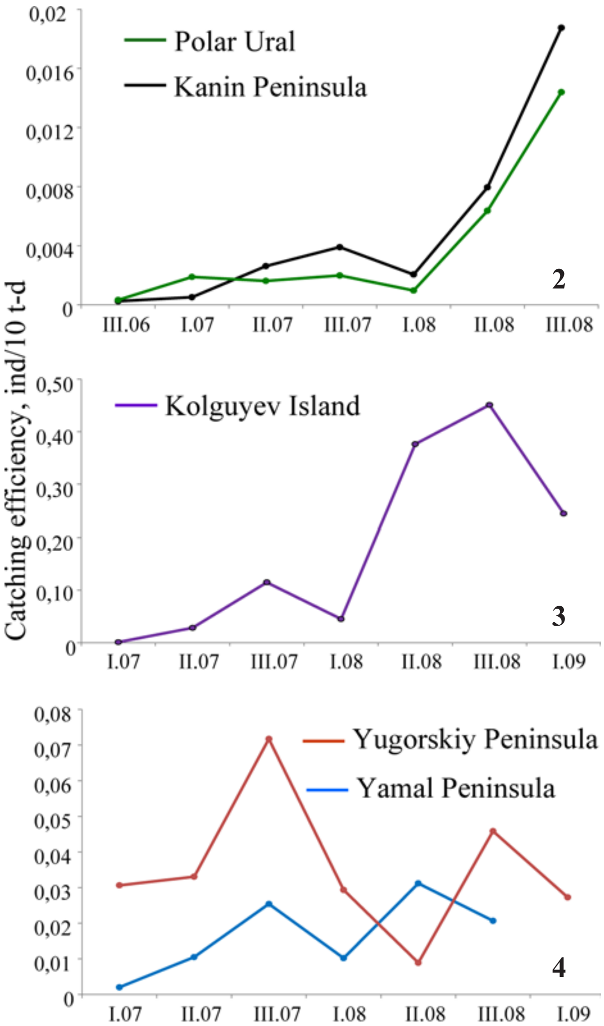


Fig. 1. Sex and age structure of the population of *D. polita* according to collecting by pitfall traps on Kolguyev Island in 2009.

Рис. 1. Поло-возрастная структура популяции *D. polita* по данным учётов почвенными ловушками на о-ве Колгуев в 2009 г.

adults were recorded from the first half of July. More than 75% of the population was represented by mature adults, in the middle of August in typical tundra (Yamal Peninsula and Kolguyev Island) (Fig. 1). Peak of mature adults in forest-tundra of Polar Ural (72% of the population) and in southern tundra of Kanin Peninsula (76% of the population) was detected in the end of August. Early peak of mature adults (91,6% of the population) in the end of July was registered for Yugorskiy Peninsula, but the second one was in time with others peaks of *D. polita* in typical tundra. Larvae of *D. polita* on Kolguev Island were catching from the second week of July to the first week of August and one peak activity was recorded in the end of July (Table 2).



Figs 2–4. Seasonal mature adults activity of *D. polita*: 2 — forest-tundra and southern tundra; 3–4 — typical tundra (see Tables 1, S1).

Рис. 2–4. Сезонная активность половозрелых имаго *D. polita*: 2 — лесотундра и южная тундра, 3–4 — типичная тундра (см. таблицы 1 и S1).

Regulation of seasonal activity

Males and females of *D. polita* became active at the same time in trapping seasons and demonstrated the common trend for all studied populations ($r = 0.91$; $n = 35$, $P < 0.001$). Seasonal activity of mature adults was different between localities and, despite different years of beetles collection, the catching efficiency of *D. polita* increase from forest-tundra (0.03 ind./10 t-d) and southern tundra (0.04 ind/10 t-d) to typical tundra (1.26–0.10 ind/10 t-d) (Figs 2–4, Table S1).

The mature adults activity is differently changed with latitude (Table 3) and increased with lightday shortening for studied populations of *D. polita* except the population of the Yugorskiy Peninsula (Table S1). Females catching efficiency was stronger correlated with day duration (from $r = -0.85$ to $r = -0.94$) than males activity (from $r = -0.79$ to $r = -0.88$). Males activity shown absence of significant association with photoperiod in typical tundra on the Yamal Peninsula ($r = -0{,}38$; $n = 7$, $P = 0{,}45$). General trend shows that peaks with maximum mature adults' activity of both sexes of *D. polita* were detected in days with 17–15 hours of lighting period and their catching efficiency is decreased in days shorter than 14 hours (Table S1). An exception was activity of mature adults from population of the Yugorskiy Peninsula. Maximal number of individuals was caught there in the end of July immediately after the end of polar day (Table S1). Seasonal change of mean air temperature did not correlate with mature adults activity (Table S1). In typical tundra the period of adult activity of *D. polita* was decreased when mean daily temperature dropped below 6° C (Table S1).

Discussion

Seasonal activity and reproduction

The seasonal activity of *D. polita* recorded in this study shows that adults were active from the end of June till September generally with a single peak in August. This activity patterns is common for populations from

Table 3. Sources of variation in mature adults' seasonal activity of *D. polita* (GLMs).
Таблица 3. Факторы, влияющие на сезонную активность половозрелых имаго *D. polita* (GLM).

Response variable	Females			Males		
	df	F	p	df	F	p
Latitude	4	14.87	0.000001	4	6.611	0.0006
Mean temperature	1	0.012	0.905	1	0.012	0.926
Polar day duration	1	12.12	0.0012	1	4.65	0.033
Latitude × Polar day duration	4	10.54	0.000017	4	4.231	0.0068
Error	25			25		

forest-tundra to typical tundra of North Europe and West Siberia. Two peaks of adults' activity in July and August were registered in typical tundra of the Yugorskiy Peninsula. Data on larval activity was scarce and have been registered in typical tundra of the Kolguyev Island from the end of July to the beginning of August and in southern tundra of the Kanin Peninsula at the same period. Mature adults were recorded from the first half of July and showed peaks of activity from the second to the third ten-day period of August. Reproduction period of *D. polita* for most of studied populations lasted three ten-days period from the end of August to the beginning of September. An activity peak of teneral beetles was detected during the reproduction period of *D. polita*. Teneral adults were also recorded at the beginning of an activity season. Third instar larvae of *D. polita* were trapped in southern tundra and typical tundra in the end of July. This fact evidences about the pupation in the beginning of August. Newly emerged beetles were registered in the end of August and they hibernate in the imaginal stage. This corresponds with catch of immature beetles in the end of August from North America by Lindroth [1961] and from August to September on the Kola Peninsula and in Norway [Hanssen, Olsvik, 1998]. Teneral beetles are reached maturity at the second part the summer of the next year.

We concluded that *D. polita* develops during two years, overwinters as larva and as adult, adult lives more than one year, and the different reproductive states and generations overlap during one seasons. Old-mature beetles participate in the reproduction and assuring the persistence of the population. Thus, according to the life-cycles typology [Matalin, 2007] *D. polita* is obligate-biennial late summer iteroparous species (Fig. 5). Our result corresponds to previous conclusions about increasing proportion of species with two-year life-cycle in carabids faunas along the latitudinal gradient to north or along the altitudinal gradient to height in mountains [Paarmann, 1979; Sota, 1994; Sharova, Filippov, 2003; Matalin, 2007]. In instance on the North of Russian Plain the proportions of carabids species with two-year life cycle rise up from 40 % in taiga to 60 % in tundra [Filippov, 2008].

Seasonal activity regulation

Mature adults activity of *D. polita* was from seven to eight ten-day periods among studied populations. Nevertheless, the highest catching efficiency of mature adults was registered in two last ten-days period of August due to photoperiod conditions. Under condition of a polar day reduction adult beetles were stimulated to maturation and reproduction, and reaching the peak activity of individuals at the time when the daylight duration reaches 17–15 hour in typical tundra and 16–15 hour in forest-tundra and southern tundra. Similar adaptation to Subarctic was studied for *Pterostichus nigrita* (Paykull, 1790). For this species the ovaries, remained undeveloped in constant long and day night duration of 2–4 hours, are still enough to enable the maturation processes in population of Northern Sweden (Lapland, 65 °N) [Thiele, 1979]. The optimal light period for *P. nigrita* was about 15 hours and the critical photoperiod is about 13 hours per 24 hours [Thiele, 1979]. For *D. polita* the day shorter than 14 hour of lighting period suppresses the mature adults activity and induces diapause in the typical tundra. Also, activity of mature females was more synchronized with photoperiod conditions than in mature males. Such pattern, with weakening of photoperiodic control of gonad maturation in males more than in females, was detected for *Pterostichus adstrictus* Eschscholtz, 1823 [Paarmann, 1994]. The both sexes of adult beetles in typical tundra of the Yugorsky Peninsula had not significant correlations with photoperiod conditions, as well as mature males from population of the Yamal Peninsula, but demonstrated common patterns of seasonal activity of *D. polita* in typical tundra. Seasonal changing of mean air temperature was not associated with adult beetles activity of *D. polita*. Photoperiodic control of gonad maturation for carabid beetles has a high influence in temperate zone and loses this influence in the Subarctic [Paarmann, 1979]. Species in the Arctic may lost reaction to a change of photoperiod and the ability of synchronizing of the egg laying period with the annual climate change gain a great importance, which was shown for *P. adstrictus* [Paarmann, 1994].

Apparently, northward distribution of *D. polita* is limited by temperature conditions of localities that pro-

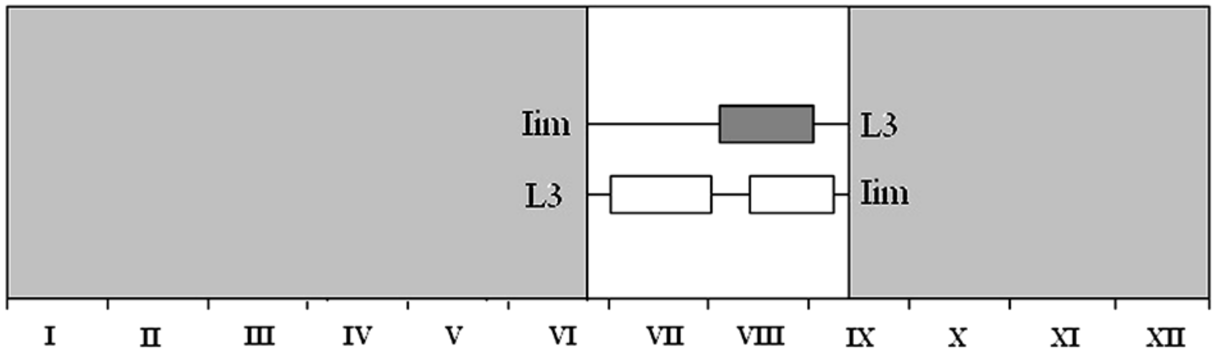


Fig. 5. Two years life cycle of *D. polita* with activity season — white color and hibernation — grey color; L3 — third instar larvae, Iim — immature; White rectangle — teneral, grey rectangle — mature.

Рис. 5. Двухгодичный жизненный цикл *D. polita* с периодом активности (белый фон) и зимней спячки (серый фон); L3 — личинки третьего возраста, Iim — неполовозрелые имаго; молодые особи обозначены белым прямоугольником, половозрезые — серым.

vide to develop within two-year life cycle and photoperiod conditions, witch regulate of seasonal activity and reproduction. So, for cold-adaptive *D. polita* with two-year life- cycle the photoperiodic regulation of maturation and breeding can restrict species distribution in high Arctic. Ability to develop without dormancy during summer or winter over a wide temperature range as found for *Pterostichus brevicornis* given more opportunity for success distribution in the Arctic [Paarmann, 1994].

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Supplementary materials

Table S1. Polar day duration, average air temperature, catching efficiency (individuals/10 trap×days) of *D. polita* of studied localities

Таблица S1. Продолжительность полярного дня, средняя температура воздуха, уловистость (особей/10 ловушек×сут) *D. polita* изученных местообитаний

Local fauna	Decade.Month	Polar day duration (hours)	Average air temperature (T, °C)	Catching efficiency of female	Catching efficiency of male
Polar Ural, 10 km from Kharp settlement	III.06	24,00	12,9	0,00066	0,00066
	I.07	23,03	12,5	0,00081	0,00161
	II.07	20,52	18,2	0,00129	0,00162
	III.07	19,09	18,9	0,00099	0,00223
	I.08	17,45	10,4	0,00121	0,00097
	II.08	16,26	10,3	0,00727	0,00879
	III.08	15,02	12,0	0,00875	0,01157
Spearman's rs*				r = -0,89; P = 0,012	r = -0,79; P = 0,048
Kanin Peninsula, Shoyna settlement	III.06	24,00	7,8	0,00000	0,00024
	I.07	24,00	6,1	0,00026	0,00026
	II.07	22,01	12,5	0,00024	0,00237
	III.07	19,45	14,4	0,00028	0,00362
	I.08	18,09	4,0	0,00103	0,00103
	II.08	16,43	6,2	0,00179	0,00615
	III.08	15,13	5,5	0,00875	0,01000
Spearman's rs				*r* = -0,94; *P* = 0,004	*r* = -0,88; *P* = 0,015
Kolguyev Island, Bugrino settlement	I.07	24,00	5,4	0,00000	0,00122
	II.07	24,00	9,0	0,00199	0,02639
	III.07	20,34	10,7	0,03833	0,07667
	I.08	18,31	7,7	0,01790	0,02716
	II.08	16,57	9,3	0,15056	0,22583
	III.08	15,30	7,4	0,20361	0,24750
	I.09	14,15	10,1	0,14207	0,10243
Spearman's rs				*r* = -0,85; *P* = 0,025	*r* = -0,84; *P* = 0,025
Yugorskiy Peninsula, Amderma settlement	III.06	24,00	12,4	0,00563	0,00985
	I.07	24,00	9,1	0,01587	0,01478
	II.07	24,00	11,9	0,01565	0,01739
	III.07	21,11	11,6	0,03326	0,03848
	I.08	18,58	8,7	0,01739	0,01196
	II.08	17,14	7,1	0,00435	0,00457
	III.08	15,32	7,6	0,02457	0,02130
	I.09	14,04	6,1	0,01712	0,01015
Spearman's rs				*r* = -0,32; *P* = 0,45	*r* = -0,12; *P* = 0,79
Yamal Peninsula, Seyakha settlement	I.07	24,00	7,2	0,00051	0,00152
	II.07	24,00	6,2	0,00401	0,00648
	III.07	21,50	8,0	0,00902	0,01639
	I.08	19,18	7,0	0,00641	0,00379
	II.08	17,28	8,2	0,01481	0,01636
	III.08	15,41	6,4	0,01204	0,00864
Spearman's rs				*r* = -0,85; *P* = 0,03	*r* = -0,38; *P* = 0,45

Legend:* Spearman's correlations between seasonal activity of mature adults and daylight duration

Легенда: * Корреляция по Спирмену между сезонной активностью взрослых взрослых особей и продолжительностью светового дня.

Table S2. Seasonal changes of age stage *D. polita* in different local fauna (individuals)
Таблица S2. Сезонная динамика репродуктивных стадии *D. polita* в разных локальных фаунах (экз.)

Local fauna	Sex	Age	Decade.Month							
			III.06	I.07	II.07	III.07	I.08	II.08	III.08	I.09
Polar Ural, 10 km from Kharp settlement	Female	t	0	0	0	0	0	8	5	13
		im	0	0	1	3	2	6	3	16
		m	1	6	4	6	2	13	33	65
		m2	0	0	0	0	0	0	0	0
		sp	0	0	0	0	0	0	0	0
	Male	t	0	0	0	1	2	15	10	28
		im	1	2	2	1	0	0	3	9
		m	0	1	1	4	2	8	18	32
		m2	0	0	0	1	0	0	0	1
		sp	0	0	0	0	0	0	0	0
Kanin Peninsula, Shoyna settlement	Female	t	0	0	0	0	0	1	1	—
		im	0	0	1	0	1	7	2	—
		m	0	1	1	1	2	6	6	—
		m2	0	0	0	0	2	1	1	—
		sp	1	0	1	0	0	1	0	—
	Male	t	0	0	0	0	0	1	0	—
		im	0	0	0	1	0	0	0	—
		m	1	1	10	13	4	24	8	—
		m2	0	0	0	0	0	0	0	—
		sp	0	0	0	0	0	0	0	—
Kolguyev Island, Bugrino settlement	Female	t	—	7	5	5	0	5	49	47
		im	—	7	108	57	0	14	21	18
		m	—	0	6	108	42	512	731	474
		m2	—	0	1	30	16	30	2	17
		sp	—	0	6	160	45	196	60	36
	Male	t	—	13	5	1	1	5	43	29
		im	—	13	48	18	0	2	5	9
		m	—	2	93	273	88	813	891	354
		m2	—	0	0	3	0	0	0	0
		sp	—	0	0	35	11	55	21	44
Yugorskiy Peninsula, Amderma settlement	Female	t	4	0	0	1	5	0	3	0
		im	28	5	0	0	9	3	27	23
		m	15	69	72	153	77	18	104	77
		m2	5	4	0	0	3	2	9	4
		sp	27	25	18	12	4	5	31	26
	Male	t	1	0	0	3	17	2	2	0
		im	13	8	0	0	5	3	12	15
		m	35	68	80	176	55	21	98	48
		m2	0	0	0	0	0	0	0	0
		sp	6	4	4	2	6	3	7	3
Yamal Peninsula, Seyakha settlement	Female	t	—	0	0	0	0	0	0	—
		im	—	16	17	4	2	7	3	—
		m	—	1	13	10	21	47	38	—
		m2	—	0	0	1	1	1	1	—
		sp	—	0	3	3	1	1	7	—
	Male	t	—	1	1	0	0	0	0	—
		im	—	10	6	1	7	1	2	—
		m	—	3	21	20	13	53	28	—
		m2	—	0	0	0	0	0	0	—
		sp	—	0	1	0	1	4	0	—

Legend: t — teneral, im — immature, m — mature, m2 — old-mature, sp — spent; «—» material was not collected
Обозначения: t — ювенильные особи, im — незрелые особи, m — половозрелые особи, m2 — повторно размножающиеся особи, sp — постгенеративные особи; «—» — материал не собирался